

ART. XVI. ARDYNOMYS AND DESMATOLAGUS IN THE  
NORTH AMERICAN OLIGOCENE

BY J. J. BURKE

(TEXT FIGURES 1-7)

Study of the fossil rodents and lagomorphs in the collections of the Carnegie Museum reveals that the genera *Ardynomys* and *Desmatolagus*, which have previously been known only from the Oligocene of Asia, are also represented in deposits of that age in western North America. Through the courtesy of Dr. Walter Granger I have been able to compare the specimens described in this paper with fossil material from Mongolia preserved in the collections of the American Museum of Natural History. The illustrations which accompany this article are taken from drawings by Mr. Sydney Prentice.

Order SIMPLICIDENTATA Lilljeborg

Family ISCHYROMYIDÆ Alston

Genus ARDYNOMYS Matthew and Granger

***Ardynomys occidentalis* sp. nov.**

*Holotype*: Right ramus of mandible with incisor, P<sub>4</sub>, M<sub>1-2</sub> and base of M<sub>3</sub>, Carnegie Museum No. 1056.

*Referred specimens*: Left ramus of mandible with broken incisor,

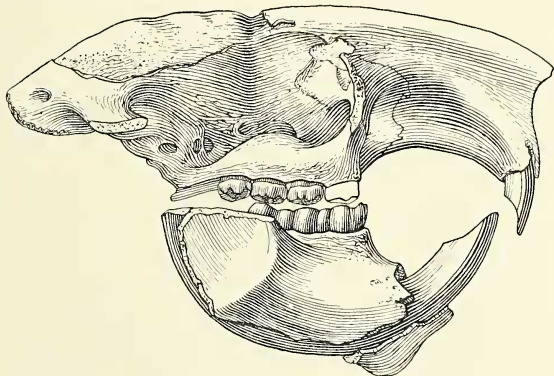


FIG. 1. *Ardynomys occidentalis* Burke. Right lateral view of skull, C. M. No. 1055 and holotype right ramus of mandible, C. M. No. 1056. Squamosal region of skull restored from left side.  $\times 2$ .

worn  $M_{1-2}$ ,  $P_4$  and  $M_3$  broken off, C. M. No. 1105; partial skull lacking  $P^{3-4}$  on both sides and with  $LM^3$  missing, C. M. No. 1055; right maxilla with root of  $P^3$ , worn  $P^4$  and  $M^{1-2}$ , C. M. No. 1083.

*Horizon:* McCarty's Mountain Oligocene.

*Localities:* C. M. Nos. 1056, 1105, "S. of McCarty's Mt.", C. M. No. 1083 "McCarty's Mt.;" C. M. No. 1055 "S. W. McCarty's Mts."<sup>1</sup> Madison County, western Montana.

*Diagnosis:* Lower jaw essentially as in *Ardynomys olsenii* Matthew and Granger, but hypoconids of molars better developed, trigonid of  $P_4$  less transverse, its cusps not as widely separated and the external valley of  $P_4$  not as crowded. Species of smaller size than *Ardynomys chihii* Matthew and Granger ( $P_4-M_3=10$  mm.).

Perhaps the most striking features of the skull (C. M. No. 1055) which I am referring to this species are the robust construction throughout, the flattened brain-case, the sharply constricted and narrow interorbital region, and the antorbital breadth, coupled with an angular and heavy type of rostrum.

Unfortunately, a great deal of the dorsal portion of the skull has been broken away, but enough remains to show that the brain-case was somewhat wider than the rostrum. The left squamosal is complete to the extent of preserving some of the characters of the glenoid fossa,<sup>2</sup> which is in general like that of *Arctomys*, broad and shallow. A small postglenoid foramen is shown, postero-median to which occurs a large subsquamosal foramen.

Despite the loss of the bones investing the brain-case dorsally, the brain cast which remains indicates that this region of the skull must have been flattened to a degree comparable with the same region in the skull of *Aplodontia*. This cast shows broad cerebral lobes and a fairly distinct superior longitudinal fissure, but the hemispheres have not the heart-shaped anterior tapering which characterizes *Cynomys*

<sup>1</sup>The locations included in quotation marks are taken directly from the field labels of these specimens. I assume that C. M. Nos. 1056, 1105 and 1083 were collected from the locality on the southeastern slope of McCarty's Mountain, about sixteen miles north and a little east of Dillon, Montana. But C. M. No. 1055 (the skull) coming from "S. W. McCarty's Mts." suggests the second locality which Earl Douglass mentions in Mem. Carnegie Museum Vol. II, No. 5, p. 211, 1905—the locality two miles west of the main collecting area. The supposition is also strengthened by the fact that of the two specimens found there, one was a *Colodon*, the other "an apparently new rodent."

<sup>2</sup>Part of this squamosal root of the zygomatic arch was accidentally shattered after Mr. Prentice had made the drawings which accompany this article.

and *Ischyromys* and, but to a lesser degree, *Aplodontia*; the outline is decidedly more rounded and becomes almost truncate directly behind the olfactory bulbs. Most of the dorsal surfaces of the olfactory bulbs appear to be exposed; they are relatively large, apparently foreshortened longitudinally, expanded laterally and inflated.

It is true that the absence of the bones of the dorsal surface of the skull probably exaggerates the interorbital constriction to some extent, but in any case it is quite pronounced. The lateral walls of the brain-case round rather sharply forward to make the constriction, anterior to which the skull again fans outward fairly rapidly to the zygomatic region. There is no means of determining, from this damaged skull whether postorbital processes were present or not; in all likelihood they were absent.

The skull under description (C. M. No. 1055) has undergone some damage in the lacrimal region; the extra-orbital part of the lacrimal bone has been lost on both sides, and there has been crushing of the skull walls within the orbits. However, on the right side, the nasolacrimal foramen is shown. The lacrimal does not enclose the canal entirely (the condition noted by Hill<sup>3</sup> in the porcupine); in general its construction seems to be as in *Arctomys*.

Of considerable interest, and particularly to be taken into account when the relationships of *Ardynomys* and the later Oligocene genera *Tsaganomys* and *Cyclomytus* are considered, is the possible incipient development, in *Ardynomys*, of an antorbital crest such as Matthew and Granger<sup>4</sup> noted in *Tsaganomys*. In anterior view the skull of *Ardynomys* shows the zygomatic region as widely expanded; even in the absence of the malar, which is not preserved in our specimens, this outjutting of the arch is pronounced. However, it is most evident below, where it would probably be accentuated if the malar were preserved. Above, the resemblance to *Tsaganomys*, as figured by Matthew and Granger, is less evident. The skull, C. M. No. 1055, upon which most of the present description is based, does not, as noted before, preserve the orbital rim entire. The maxillary, C. M. No. 1083, preserves a little more of the rim. Judging from these two specimens, the skull of this species had not yet developed an orbital ridge

<sup>3</sup>Hill, John Eric, "The Cranial Foramina in Rodents." Jour. of Mamm. Vol. 16, No. 2, p. 123, 1935.

<sup>4</sup>Matthew, W. D., and Granger, Walter, "New Bathyergidae from the Oligocene of Mongolia." Amer. Mus. Novit. No. 101, p. 3, 1923.

comparable with that of *Tsaganomys*; there appears to have been no marked or abrupt building out of the orbits above the zygomatic root, but there seems nothing to preclude the development of the ridge in the later history of a skull of this type.

The orbital and zygomatic regions of *Ardynomys occidentalis* m. do not show a great deal in the way of specialization beyond the same regions in, say, *Aplodontia*; there is a strong lateral expansion of the anterior zygomatic root, but the latter is heavy and sturdy, not thin and sharp as in *Tsaganomys*. In another feature the zygomatic structure deviates from that found in either *Aplodontia* or *Tsaganomys*; the upward tilt of the zygoma is more marked than in either of these two genera. The infraorbital foramen is somewhat ovate, as in *Tsaganomys*. I cannot find any evidence that the infraorbital foramen (which is not enlarged) transmitted a slip of the masseter.

The rostrum, seen from above, appears unusually heavy; it is quite broad posteriorly and tapers fairly uniformly anteriorly. The premaxillaries reach to the interorbital region; the premaxillary-frontal suture is shown on the right side of C. M. No. 1055, a little posterior to the naso-lacrimal foramen.

The nasals are not preserved, but the right nasal must have been broken away practically along the suture between it and the premaxillary. Assuming that the nasals were flattened, or but slightly arched, the rostrum must have presented a crudely hexagonal transverse section (similar to that of *Tsaganomys*); there is a prominent incisive swelling produced by a sharp outward arching of the premaxillaries; below the incisive swelling the sides of the rostrum have a long slope downward and inward to the palatal surface.

Of the antero-posterior extent of the palate, the premaxillaries constitute about a third. An interpremaxillary foramen is not definitely indicated; if present it must have been quite small. The palate narrows posterior to the incisors but expands again about the middle of the rostrum. The incisive foramina are of fair size and confined to the premaxillaries. The tooth rows diverge anteriorly; the palate is broadest in the region of the premolars. The posterior palatal notch extends anteriorly to the posterior region of M<sup>2</sup>; the palatines are short. A median ridge extends the length of the palate anteriorly as far as the anterior palatine foramina; it is flanked on either side by rather vague ridges bordering the alveoli of the cheek teeth. In the

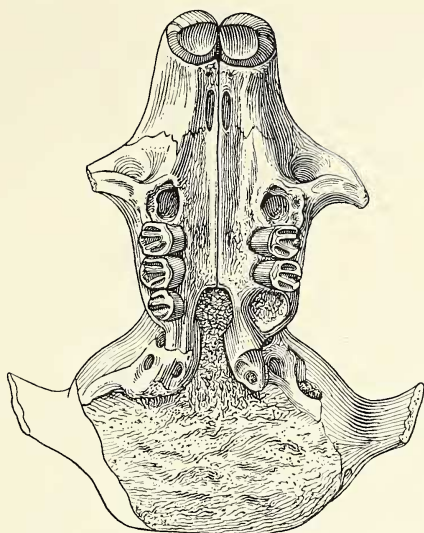


FIG. 2. *Ardynamys occidentalis* Burke. Ventral view of skull, C. M. No. 1055. Left side of rostrum restored from opposite side.  $\times 2$ .

two channels separating these ridges the slit-like posterior palatine foramina are located opposite the first molars.

Crushing and distortion makes the determination of some of the cranial foramina rather tentative. From its position in what appears to be the pterygoid fossa I take the foramen which shows in ventral view to be the sphenopterygoid. A foramen showing external to the fossa, and dorsal to the last, which is directed posteriorly in the alisphenoid, would appear to be the masticatory. In advance of the latter appear two openings in the region of the sphenoid fissure; the posterior of these must be the anterior exit of the sphenopterygoid + the alisphenoid canals. The opening in advance of this seems to be the sphenoid fissure proper. Further forward, and well separated from the last, is found the prominent optic foramen.

The incisors of this form are especially large when compared with the cheek teeth. The superior incisors are flattened along the anterior surface (showing only a slight rounding) and are a little more extended transversely than antero-posteriorly. On the sides of the rostrum the courses of the incisors are indicated by well-defined incisive swellings.

In the skull, C. M. No. 1055, the cheek teeth anterior to the molars are not shown. However, in a maxilla, C. M. No. 1083, P<sup>4</sup> is preserved, although somewhat broken, and the root of P<sup>3</sup> is also retained. The latter tooth was quite small—merely a slender spike which rested



FIG. 3. *Ardynomys occidentalis* Burke. Occlusal view showing root of P<sup>3</sup>, and worn P<sup>4</sup>, M<sup>1-2</sup> right, C. M. No. 1083.  $\times 4$ .

along the antero-internal side of P<sup>4</sup>. P<sup>4</sup>, on the other hand, was the largest tooth in the maxilla. As exhibited in this specimen it is badly worn, showing a broad shelf of wear on the internal side. Externally, however, most of the original crown structure can be made out. Traces of the anterior and posterior valleys remain; the posterior valley (now represented by a shallow and small fossete) was apparently the larger of the two. Worn cusps represent the paracone and the metacone, from which converging lophs extend toward the worn internal shelf. Separating these lophs appears a broad V-shaped central valley, the outlet of which is blocked by two low intermediate tubercles conjoined at their bases.

In the skull, C. M. No. 1055, the alveolus for P<sup>4</sup> indicates a three-rooted tooth commensurate in size with P<sup>4</sup> of C. M. No. 1083. In advance of the internal root socket of this tooth appears the alveolus for a small tooth occupying the same position as P<sup>3</sup> in C. M. No. 1083.

The cheek teeth of *Ardynomys occidentalis* m. combine unilateral hypsodonty (by extension rootward of the crown enamel of the protomere) with oblique implantation (the plane of the superior tooth row slants outward, that of the inferior tooth row slants inward, in both cases strongly oblique to the vertical plane of the skull). The combined effect of these dental constructions is the conservation of the enamel of the tooth with wear. With age, the teeth of *Ardynomys occidentalis* m. show marked broadening of the protomere shelf, the crown surface of which is worn away long before that of the metamere.

The molars of the skull, C. M. No. 1055, show little wear. Seen at the crown surface they are subrectangular in outline. They taper somewhat rootward (especially M<sup>1</sup>) when viewed internally. At the

present stage of wear  $M^{1-2}$  have the same crown dimensions, but  $M^2$ , being more rounded below, might be expected to vary from  $M^1$  at a later stage of wear.  $M^3$  is reduced in size over  $M^{1-2}$ .

The molar pattern on the external side follows the same general plan as that described for  $P^4$ , consisting of anterior and posterior



FIG. 4. *Ardynomys occidentalis* Burke. Occlusal view of  $RM^{1-3}$ , C. M. No. 1055.  $\times 4$ .

cingular crests, separated by anterior and posterior valleys from the protoloph and the metaloph. The latter lophs converge and extend to the internal shelf in the form of a sharp V, enclosing between them the central valley. The shelf is not strongly bowed in outline at the crown surface, though, a feature which contributes to the sub-rectangular outline of these teeth. In all of the molars the metaloph is somewhat oblique to the protoloph. The external outlets of the anterior and posterior valleys are nearly completely dammed off (except in  $M^3$ , where the posterior valley exit cuts rather deeply), and are short notches considerably above the level of the central valley exit. The exits of the posterior valleys are in reality postero-external, internal to the metacones. The posterior valley extends further internally in these molars than does the anterior valley. The paracone and the metacone are nearly the same size in  $M^1$  but the paracone is in excess of the metacone in  $M^{2-3}$ . There is a small intermediate tubercle in the outlet of the anterior valley of  $RM^2$  which is not present in that place in  $LM^2$ . There is an intermediate tubercle in the outlet of the central valley of  $M^1$  which forms a dam; the same condition holds in  $M^2$ . In  $M^3$  the intermediate tubercle is not present, but a small tubercle buds off the posterior flank of the metacone, somewhat crowding the exit of the posterior valley. A definite metaconule is not shown in  $M^1$  or in  $M^2$  although some swelling of the metalophs probably indicates it. In  $M^3$  it is indicated as a vanishing tubercle on the unworn metaloph. Incidentally, the metaloph in  $M^3$  sinks below the level of the triturating surface before connecting with the internal shelf—a condition which may have held, to some extent, in the metalophs of  $M^{1-2}$  before they were worn down. On the internal side, the molars show slight anterior

and posterior enamel grooves or notches, between which the protocone swells internally.

The lower jaw, except for its smaller size, is remarkably close to that of *Ardynomys olseni* M. & G. In both cases the jaws are heavy and are deep anteriorly; the masseteric fossa is not in advance of  $M_1$ . Ventrally the symphysis is extended downward to produce a sharp flange-like projection. There is a large mental foramen, below and just anterior to  $P_4$ . The American form agrees with *Ardynomys olseni* M. & G. and *Ardynomys chihi* M. & G., in showing the ramus much pinched from the external side in the region of the diastema. The diastema has about the same relative extent as in *Ardynomys olseni* M. & G.

The lower incisor is very much like that of *Ardynomys olseni* M. & G. It shows the flattened anterior face characteristic of the genus, and the incisor of the holotype, C. M. No. 1056, shows the shallow grooving or concavity on the anterior face, noted by Matthew & Granger.<sup>5</sup> This grooving is not apparent in the incisors of the referred specimen, C. M. No. 1105.

As in *Ardynomys olseni* M. & G. the mandibular cheek teeth are not only oblique to the antero-posterior plane of the ramus, the



FIG. 5. *Ardynomys occidentalis* Burke, holotype. Occlusal view of  $P_4$ ,  $M_{1-2}$  right, C. M. No. 1056.  $\times 4$ .

tooth rows converging posteriorly, in keeping with the maxillary tooth rows, but also they are implanted obliquely to the vertical plane of the ramus, and overhang on the internal side.

$P_4$  of *Ardynomys occidentalis* m., as shown in the holotype, bears on the trigonid two cusps, which are separated by a notch-like median valley anteriorly. The internal of these two cusps is the larger and doubtless was, before wear, the higher of the two, as in *Ardynomys olseni* M. & G. Its posterior flank is considerably drawn out to meet with the base of the postero-internal cusp, raising the internal outlet

<sup>5</sup>Matthew, W. D. and Granger, Walter, "New Creodonts and Rodents from the Ardyn Obo Formation of Mongolia." Amer. Mus. Novit. No. 193, p. 5, 1925.



of the central basin high above the floor of the basin. The antero- and postero-external cusps are connected by an ectolophid.

The hypoconid is an over-sized, jutting cusp, becoming a shelf with wear. From it extends a hypoconulid crest which sweeps around to join with the entoconid. The central basin is broad and rounded, and there is no definite evidence of any crests from the trigonid cusps within it. Also, at first glance, there appears to be no hypolophid crest present. However, on close inspection it can be detected forming the posterior boundary of the central basin. It is low, curling parallel with the hypoconulid crest, and is evidently being eliminated, although it still shows a connection with the entoconid. The posterior valley is little more than an entrenched shelf behind it. The illustration of the type of *Ardynomys olseni* M. & G.<sup>6</sup> does not depict a hypolophid in  $P_4$ . I have not checked the accuracy of the drawing, but  $P_4$  of A. M. No. 20369, a specimen referred to *Ardynomys olseni* M. & G. shows a hypolophid very much like that in  $P_4$  of the specimen under description—with the exception that it is perhaps better developed. I have at hand also one of the paratypes of *Ardynomys chihi* M. & G., A. M. No. 20372, which shows a stubby but well-defined hypolophid in  $P_4$ . The illustration of the holotype of this species does not indicate a hypolophid in  $P_4$  either.<sup>7</sup>

The cheek teeth increase in size from  $P_4$  to  $M_2$ ;  $M_3$  was considerably smaller than  $M_2$  ( $M_3$  is represented only by the roots in both the holotype, C. M. No. 1056, and in the referred specimen, C. M. No. 1105). The molars of C. M. No. 1105 are so worn as to obliterate all details of the crown pattern at the occlusal surfaces. The holotype, however, still preserves the central valleys on  $M_{1-2}$ ; the valleys have a V-shape with wear, and at their outlets are flanked by the entoconids and metaconids; the entoconids, on  $P_4$ ,  $M_1$  and  $M_2$ , do not extend as far internally as do the metaconids. On  $M_1$  of C. M. No. 1056 I can detect the last traces of the posterior valley. Judging from what is preserved of the pattern, though, and from the configuration of the teeth in general, the unworn crown must have resembled rather closely that of *Ardynomys olseni* M. & G. In general construction the molars as now preserved, except for more transverse trigonids, resemble  $P_4$ . The oversized hypoconids are broad shelves, which bore the brunt of wear. The hypoconid juts strongly externally

<sup>6</sup>*Ibid*, text fig. 8 (p. 6).

<sup>7</sup>*Ibid*, text fig. 9 (p. 7).

in  $M_1$  (more so than in  $P_4$ ) and still more prominently in  $M_2$ . Not only is the hypoconid a greatly enlarged element of the crown in these teeth, but also the enamel extends disproportionately down along its enlarged root; one is tempted to call this "unicuspal," rather than unilateral, hypsodonty.

The above characters might well serve as an enumeration of those which also show in the worn lower cheek teeth of *Ardynomys olseni* M. & G. or of *A. chihi* M. & G. To a considerable degree they also apply to those of *Pseudocylindrodon neglectus* m. and to *Sespemys thurstoni* Wilson. In a previous paper,<sup>8</sup> I have pointed out some of the differences which exist between *Ardynomys* and *Pseudocylindrodon*:

"In some respects, *Pseudocylindrodon* is intermediate between *Cylindrodon* and *Ardynomys*. The cheek teeth are nearer those of *Ardynomys* in crown height and their tendency toward hypertrophy of the hypoconid regions; the tooth pattern in general shows similarities. The incisor of *Pseudocylindrodon* is not flattened, however, as it is in *Ardynomys*; the central basins of the cheek teeth are deeper in *Pseudocylindrodon*, have rounded floors, and are closed internally by the upgrown intermediate cuspule. The jaw of *Ardynomys* is deeper anteriorly than that of *Pseudocylindrodon*, the posterior basins of the cheek teeth of *Ardynomys* have internal exits, and the protolophids are less transverse than in *Pseudocylindrodon*."

It might be added to the above, however, that *Ardynomys chihi* M. & G. shows the central valley of  $M_3$  closed off on the internal side. Matthew and Granger state that it is "closed by a marginal inner crest."<sup>9</sup> On  $M_3$  of one of the paratypes, A. M. No. 20371, the intermediate tubercle is still indicated as an element in this crest—so that the closure of the central valley in this tooth has come about in essentially the same manner as in the inferior molars of *Pseudocylindrodon neglectus* m. The intermediate tubercle is still indicated on  $M_{1-2}$  of A. M. No. 20371, also, where it is fused below with the posterior flank of the metaconid. Incidentally, this same paratype shows an accessory cuspule in the posterior valley of  $M_3$ , and a spur crossing the central valley from the hypolophid to the metaconid in

<sup>8</sup>Burke, J. J., "Pseudocylindrodon, a New Rodent Genus from the Pipestone Springs Oligocene of Montana." Ann. Carn. Mus. Vol. 25, Art. 1, p. 3, 1935.

<sup>9</sup>Matthew, W. D. and Granger, Walter, "New Creodonts and Rodents from the Ardyn Obo Formation of Mongolia." Amer. Mus. Novit. No. 193, p. 7, 1925.

the same tooth. This spur had its origin in two tubercles, a small one on the anterior side of the hypolophid, a larger one at the base of the metaconid; the two have fused, but are still indicated. In  $M_2$  the tubercles are present but not joined. They are also apparent in  $M_1$ , but are rather poorly shown. Another paratype, A. M. No. 20372, preserves  $P_4$ , and as I have mentioned previously in this article, a short hypolophid is present. The entoconid in  $P_4$  of this specimen is quite well-defined and attenuated externally to meet the hypolophid. Apparently *Ardynomys chihi* M. & G. is a well established species, quite distinct from *Ardynomys olseni* M. & G., and probably, as regards the pattern at least, even further removed from the latter species than is *Ardynomys occidentalis* m.

At the time of the description of *Pseudocylindrodon neglectus* m. I had not seen Wilson's excellent description and illustrations of *Sespemys thurstoni*.<sup>10</sup> *Sespemys*, in several respects, shares characters with both *Pseudocylindrodon* and *Ardynomys*. *Sespemys* tends toward hypertrophy of the hypoconid as do *Pseudocylindrodon* and *Ardynomys*; in depth of lower jaw it seems nearer *Pseudocylindrodon* than *Ardynomys*, it preserves the internal intermediate tubercle of the molars, found also in *Pseudocylindrodon* and in *Ardynomys chihi* M. & G., although the tubercle in *Sespemys* tends to be attenuated into the central valley as a sort of spur—a condition which I have not noted in *Pseudocylindrodon* and *Ardynomys*. The tubercle in *Sespemys* does not appear to fuse with the metaconid and the entoconid to block the central valley as it does in  $M_{1-3}$  of *Pseudocylindrodon* and in  $M_3$  of *Ardynomys chihi* M. & G. *Sespemys* preserves the protolophid in  $P_4$ , the protolophid does not appear to occur in  $P_4$  of *Ardynomys*, there are only traces of it in  $P_4$  of *Pseudocylindrodon*, if it is indicated at all. *Sespemys* shows short molar protolophids which compare better with those of *Ardynomys* than with the molar protolophids found in *Pseudocylindrodon*. The hypolophid seems well developed in  $P_4$  of *Sespemys*; it is present, but shows poor development, in  $P_4$  of *Ardynomys*; it is absent in *Pseudocylindrodon*. The posterior valley of the molars is open in *Sespemys*, open but crowded in *Ardynomys*, definitely closed in *Pseudocylindrodon*. In depth of valleys, the molars of *Sespemys* appear to be nearer to those of *Ardy-*

<sup>10</sup>Wilson, Robert W. "Two Rodents and a Lagomorph from the Sespe of the Las Posas Hills, California." Carn. Inst. Wash., Publ. 453, No. 2, pp. 13-16, text fig. 1, pl. 1, figs. 2, 2a, 2b, 1934.

*nomys*, the molar valleys of neither of those two forms seem as deep as those of *Pseudocylindrodon*. The anterior face of the incisor is flattened in *Sespemys* and in *Ardynomys*, rounded in *Pseudocylindrodon*. All three genera agree in showing an enlarged central valley and reduced posterior valley, and in having hypolophid crests that are transversely shortened.

From the above intermingling of characters I conclude that *Sespemys*, *Ardynomys* and *Pseudocylindrodon* are rather closely related genera. Wilson has observed,<sup>11</sup> in *Sespemys*, and Matthew and Granger have pointed out,<sup>12</sup> in *Ardynomys* various *Ischyromyid* features. Matthew and Granger, stated<sup>13</sup> of *Ardynomys*, that its teeth "retain the partly subcircular outlines of *Tillomys* and have not taken on the rectangular proportions of *Ischyromys*, but the relationships of the genus are probably with this family, as Troxell has also urged for *Tillomys*." When distinguishing *Pseudocylindrodon* from *Cylindrodon*, I found the two genera had much in common with *Ardynomys*, and remarked that "*Cylindrodon*, *Pseudocylindrodon* and *Ardynomys* are probably Oligocene representatives of the stock of rodents typified in the Bridger Eocene by the forms which Troxell has included under *Tillomys*."<sup>14</sup> To the "Oligocene representatives" I believe that we should now add *Sespemys*.

In deriving these genera from the *Tillomys* stock, and in suggesting their interrelationships, I am basing my conclusions on certain fundamental cusp-crest details of the tooth pattern which characterize *Tillomys* and *Tillomys*-like rodents of the Eocene—characters which in these Oligocene forms have undergone alterations, modifications of the *Tillomys* dental mechanism that fitted the group for invasion of certain environmental locales which during the Eocene appear to have been generally the province of various rodents of the *Paramys* group. Possibly, during the Eocene, the *Tillomys* stock was predominantly arboreal, its diet principally one of seeds and fruits; the same may have been true for the majority of the *Paramyidae*. But

<sup>11</sup>Wilson, Robert W., "Two Rodents and a Lagomorph from the Sespe of the Las Posas Hills, California." Carn. Inst. Wash., Publ. 453, No. 2, p. 15, 1934.

<sup>12</sup>Matthew, W. D. and Granger, Walter, "New Creodonts and Rodents from the Ardyn Obo Formation of Mongolia." Amer. Mus. Novit., No. 193, p. 5, 1925.

<sup>13</sup>*Ibid.*

<sup>14</sup>Burke, J. J., "Pseudocylindrodon, a New Rodent Genus from the Pipestone Springs Oligocene of Montana." Ann. Carn. Mus., Vol. 25, Art. 1, p. 3, 1935.

by Bridger time certain of the members of the *Paramys* stock developed specializations of the dental mechanism and skeleton which point to a terrestrial life. In Matthew's *hians* group<sup>15</sup> characterized by "broad robust molars" and wide incisors we find a departure from the more typical Paramyid dentition, and an increase in body size, which might indicate trends toward a coarser vegetable diet and better adaptability for a semi-arboreal, perhaps terrestrial, existence. Later, in the Uinta, we find *Ischyrotomus* (which Matthew suggested may have been derived from the *hians* group<sup>16</sup>) attaining maximum size for the *Paramyidæ*; its skeleton indicates not only a terrestrial but also even a fossorial habitat.<sup>17</sup> *Ischyrotomus*, incidentally, furnishes an instructive comparison with *Ardynomys*. In both genera the skulls are stoutly constructed and robust, and Matthew's description of the muzzle of *Ischyrotomus petersoni* as "peculiarly angular" might also apply to the skull of *Ardynomys*. The lower jaws in both genera are heavy. *Ardynomys olseni* M. & G. and *occidentalis* m. develop a flange-like downward extension in the symphyseal region of the mandible not altogether unlike that in *Ischyrotomus*. The incisors are flattened in both genera. The broadening of the molar basins is of course evident in *Ardynomys* as well as in *Ischyrotomus*, hypertrophy of the hypoconid region characterizes the lower molars of *Ischyrotomus*, and I might add that there is some unilateral heightening of the cheek tooth crowns in *Ischyrotomus* also. Yet the possession of these characters by the two genera in common seems nothing more than another interesting case of parallelism; they are to be found in various combinations in a number of terrestrial or fossorial rodents, both living and extinct. *Ardynomys* is removed from any close relationship with *Ischyrotomus* through the cusp-crest pattern of its cheek teeth, already complicated beyond that of *Ischyrotomus* before being secondarily modified along the same lines as in the Paramyid.

With the passing of the specialized *Paramyidæ* at the close of the Eocene it is reasonable to suppose that faunal places were open for the invasion of the *Ischyromyidæ* which, even in the Bridger, gave evidence

<sup>15</sup>Matthew, W. D., "On the Osteology and Relationships of Paramys, and the Affinities of the Ischyromyidæ." Bull. Amer. Mus. Nat. Hist. Vol. 28, Art. 6, p. 50, 1910.

<sup>16</sup>*Ibid*, phylogenetic chart, p. 51.

<sup>17</sup>*Ibid*, pp. 56-57.

of considerable plasticity. *Ardynomys* and its relatives probably replaced the *hians* group of the *Paramyidae* in the North American Oligocene, at least, and *Ardynomys* seems particularly well fitted to have superseded *Ischyrotomus*, with which it possessed a number of habitus characters in common.

## MEASUREMENTS

Holotype, Carnegie Museum No. 1056

	mm.
Diastema.....	5.0
Incisor antero-posterior.....	3.2
Incisor transverse.....	2.6
P <sub>4</sub> antero-posterior.....	2.3
P <sub>4</sub> transverse.....	2.2
M <sub>1</sub> antero-posterior.....	2.2
M <sub>1</sub> transverse.....	2.8
M <sub>2</sub> antero-posterior.....	2.6
M <sub>2</sub> transverse.....	2.7
Tooth row at alveoli.....	10.0
Molars at alveoli.....	7.7

Carnegie Museum No. 1105

Diastema.....	5.2
Incisor antero-posterior.....	3.7
Incisor transverse.....	2.8
M <sub>1</sub> antero-posterior.....	2.5
M <sub>1</sub> transverse.....	3.1
Tooth row at alveoli.....	10.0
Molars at alveoli.....	7.5

Carnegie Museum No. 1055

Height of skull measured at M <sup>1</sup> .....	13.5+
Greatest width of muzzle.....	13.0
Width of interorbital constriction.....	6.9
Diastema.....	8.4
Width of palate at P <sup>3</sup> .....	4.9
Width of palate at M <sup>3</sup> .....	4.2
Length of palate from incisors to post-palatal notch.....	10.3
Incisor antero-posterior.....	2.4
Incisor transverse.....	2.5
M <sup>1</sup> antero-posterior.....	2.1
M <sup>1</sup> transverse.....	2.3
M <sup>2</sup> antero-posterior.....	2.1
M <sup>2</sup> transverse.....	2.3
M <sup>3</sup> antero-posterior.....	1.6

	mm.
M <sup>3</sup> transverse.....	1.6
Tooth row at alveoli.....	9.1
Molars at alveoli.....	6.4

Carnegie Museum No. 1083

P <sup>4</sup> antero-posterior.....	2.5
P <sup>4</sup> transverse.....	3.8
M <sup>1</sup> antero-posterior.....	2.0
M <sup>1</sup> transverse.....	3.0
M <sup>2</sup> antero-posterior.....	2.1
M <sup>2</sup> transverse.....	2.8

### Order DUPLICIDENTATA Illiger

#### Family LEPORIDÆ Gray

#### Genus DESMATOLAGUS Matthew and Granger

#### ***Desmatolagus dicei*\* sp. nov.**

*Holotype*: Left maxillary with P<sup>3-4</sup>, M<sup>1-2</sup>; right ramus of mandible with P<sub>4</sub>, M<sub>1-3</sub>; left ramus of mandible with M<sub>1-2</sub>; C. M. No. 814.

*Horizon*: Pipestone Springs Oligocene.

*Locality*: Pipestone Springs, Jefferson County, Montana.

*Diagnosis*: Species larger than *Desmatolagus robustus* M. & G.; premolars not as well developed, molars less reduced; external outline

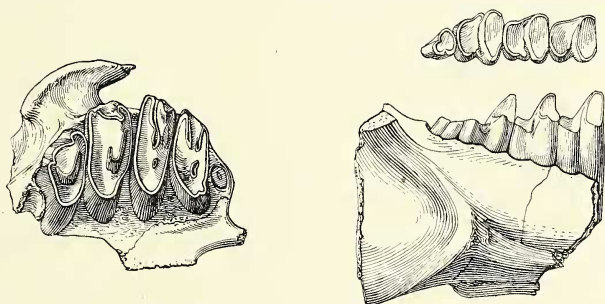


FIG. 6. *Desmatolagus dicei* Burke, holotype. Ventral aspect of left maxillary with P<sup>3-4</sup>, M<sup>1-2</sup>, occlusal view of P<sub>4</sub>, M<sub>1-3</sub> right and lateral view of right ramus of mandible, C. M. No. 814. × 2.

\*This species is named in honor of Dr. Lee R. Dice, in appreciation of his works on fossil Duplicidentates.

of maxillary tooth row more evenly rounded;  $M_2$  the largest inferior cheek tooth.

***Desmatolagus gazini*\* sp. nov.**

*Holotype*: Left maxillary with  $P^{3-4}$ ,  $M^{1-2}$ ; C. M. No. 37.

*Horizon*: Oreodon Beds Oligocene.

*Locality*: Badland Creek, Sioux County, Nebraska.

*Diagnosis*: Species intermediate in size between *Desmatolagus gobiensis* M. & G. and *Desmatolagus robustus* M. & G.; external outline of maxillary tooth row less rounded than in *Desmatolagus dicei* m. and premolar-molar proportions nearly as in *Desmatolagus robustus* M. & G. and *Desmatolagus gobiensis* M. & G., but  $P^3$  not as compressed along its anterior side and  $M^2$  with unusually short posterior wall crest, external roots of superior cheek teeth stronger.

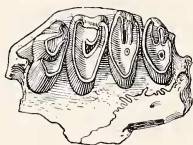


FIG. 7. *Desmatolagus gazini* Burke, holotype. Ventral aspect of left maxillary with  $P^{3-4}$ ,  $M^{1-2}$ , C. M. No. 37.  $\times 2$ .

It would appear that species of *Desmatolagus* in the North American Oligocene may be distinguished from contemporary species of *Megalagus* by their lower-crowned and more transverse cheek teeth, reduced  $M^3$  and somewhat simpler  $P^3$ . In the lower Oligocene the excess in size of  $M_2$  over  $M_1$  and  $P_4$  may also prove characteristic of *Desmatolagus*, but at present I am not inclined to place much trust in this peculiarity. It may be anticipated that when the third lower premolars of *Desmatolagus dicei* m. and *D. gazini* m. are found they will also show more reduction and secondary simplification than in *Megalagus*, while  $P^2$  may be expected to show more reduction also.

While *Desmatolagus* in the lower Oligocene in general resembles *Megalagus*, the two genera do not keep apace in their later development. Middle and Upper Oligocene species of *Megalagus* strongly

\*The specific name is in recognition of the fossil lagomorph studies of Dr. C. Lewis Gazin.



parallel *Palæolagus* in the "modernization" of their tooth structure. *Desmatolagus*, however, continues the reduction of  $M_3^{\frac{3}{2}}$  and if not the reduction, certainly the simplification of  $P_3$ ;  $P^2$  appears to be reduced and there are changes in the pattern of  $P^4$  (this tooth also undergoes compression along its anterior face). There is some equalizing of the proportions of  $P^{3-4}$  and  $M^{1-2}$ , perhaps better expressed as due to the increase in size of the premolars concerned. There seems to be, as regards the premolars at least, an increase in hypsodonty (Teilhard de Chardin<sup>18</sup> even describes  $P_3^{\frac{3}{2}}$  of his *Desmatolagus pusillus* as of continuous growth). But it is noteworthy that *Desmatolagus* also preserves, in the Upper Oligocene, an assemblage of characters which are found in the Eocene *Mytonolagus* and also in specimens of *Megalagus* from the lower Oligocene—curved superior cheek tooth shafts, relatively poorly developed unilateral hypsodonty, transverse cheek teeth and persistence of the crown pattern with wear. Certain of the above characters have doubtless been interpreted by some authors as indicative of Ochotonid affinities of *Desmatolagus*. To my way of thinking they are merely retained primitive characters, indicative of the unprogressiveness of the genus as a whole.

That lower jaws of the type which Viret<sup>19</sup> describes and figures as of *Amphilagus antiquus* closely resemble those of *Desmatolagus* goes without saying, and judging from what I can learn of these forms they must have a close relationship with *Desmatolagus*. But from the same deposits Viret has also described and figured<sup>20</sup> certain maxillaries upon which he bases his genus *Piezodus*, and these maxillaries also resemble those of *Desmatolagus*. On the other hand, the maxillaries which Viret refers to *Amphilagus antiquus*, and the lower jaws which he includes under *Piezodus brannsatensis* Viret, do not appear at all to be of the *Desmatolagus* type. Unfortunately, I do not possess any of these European forms for comparison with *Desmatolagus*, and I can only judge them from the scant literature at my disposal. I have the feeling that there has been some confusion of genera in Viret's treatment of his material. The lower jaws which

<sup>18</sup>Teilhard de Chardin, P., "Description des Mammifères Tertiaires de Chine et de Mongolie." Ann. Pal. tome XV, p. 23, 1926.

<sup>19</sup>Viret, J., "Les Faunes de Mammifères de l'Oligocène Supérieur de la Limane Bourbonnaise." Ann. Univ. Lyons, N.S. fasc. 47, pp. 85-88, et seq. text fig. 11, Pl. 29, figs 12, 13a, 13b, 14, 1929.

<sup>20</sup>*Ibid*, text fig. 14, b, b', c, c', d, e, Pl. 29, figs. 15a, 15b, pp. 94-96.

he refers to *Amphilagus antiquus*, and the maxillaries which he places in *Piezodus brannsatensis* Viret might possibly belong in the same genus or even species. The resemblance of this material to *Desmatolagus* is so well marked that I suspect that here we have European representatives of the *Desmatolagus* stock. But it does not follow, of necessity, that the mere presence of *Desmatolagus*-like forms in the European Oligocene presumes a "Lagomyid" and therefore Ochotonid disposal of the *Desmatolagus* line. From present evidence, *Desmatolagus* (and Viret's material mentioned immediately above) appear to me to have far too many characteristics of the *Leporidae* to be ancestral to any *Ochotonidae* or to warrant their inclusion in the latter family.

*Desmatolagus* is already specialized along the lines of the *Leporidae* in the pattern of its cheek teeth. Despite the marked persistence of the internal valley in  $P_4$  and in the inferior molars (a condition which, by the way, can be found in certain species of *Palaolagus*, even in the Upper Oligocene) these inferior cheek teeth are thoroughly leporine as regards their construction; they show the characteristic crowding of the paramere cusps and a main valley extending transversely across the tooth from the protomere which separates the trigonid from the talonid. In the *Ochotonidae* the paramere cusps are widely separated, and while both the internal and the external valleys appear to have conjoined to form the separation between the trigonid and the talonid, it is of note that the external valley is directed postero-internally, while the internal valley is directed antero-internally, becoming confluent with the external valley by cutting across the latter in advance of its postero-internal channel. The superior molars of *Desmatolagus* show a narrow internal notch or valley, such as characterizes the *Leporidae* generally, and the course of the valley is postero-external, or at the most transverse, not in advance of the "crescent"; the external portion of the valley becomes isolated as an enamel island as in *Mytonolagus*, *Megalagus*, and *Palaolagus*. In the *Ochotonidae* the internal cusps of the molars are well separated by a wide internal valley which is antero-externally directed, and which in the earlier forms is seen to be directed anterior to the "crescent."<sup>21</sup>

<sup>21</sup>But this "crescent," or main lunate valley, in the *Ochotonidae* may be an entirely different crown element from that called the "crescent" in the *Leporidae*. J. Ehik, in Ann. Mus. Nat. Hungarici, Vol. 23, pp. 178-186, figs. 1-5, 1926, de-

(Continued on next page)

The type of pattern torsion exhibited in the *Ochotonidæ* is not without parallels among the simplicidentate rodents; something very much like it is found among the *Castoridæ*, where it is associated with considerable preservation of the original elements of a complex talon-talonid pattern. I am inclined to think that the *Ochotonidæ*, too, retained some of the talon-talonid elements of the crown pattern longer than did the *Leporidæ*. Atrophy and fusion of the various crown elements of these regions appear to have been early developments in the *Leporidæ*, and certainly must have had their initiation well back in the history of the group, as a preliminary to the attainment of the basic leporine pattern which is already well established by Upper Eocene time.

(MEASUREMENTS ON FOLLOWING PAGE.)

scribes and figures as *Titanomys fontannesii* two maxillaries which preserve excellent details of the crown pattern. In  $P^4$  and  $M^{1-2}$  of his material Ehik found what appears to be the last trace of an anterior valley in *advance* of the main lunate valley. The internal valley in his specimens is directed antero-externally, as in *Ochotonidæ* generally, and is anterior to the main lunate valley, but is *posterior* to the presumed vestige of an anterior valley. I do not agree with Ehik's interpretation of molarization of the premolars in the *Duplicidentata*, and I am not in accord with him in his cusp terminology in general as he has applied it in this case, as I have stated in a previous article (Ann. Carn. Mus., Vol. 23, Art. 9, p. 408, 1934). But if the structure anterior to the lunate valley in  $P^4$  and  $M^{1-2}$  of Ehik's specimens is a vestigial anterior valley, then it must correspond to the anterior valley in the *Leporidæ*, and the wall which separates it posteriorly from the main lunate valley may very well represent the paracone, with which Ehik identifies it. Such a disposition of the paracone would seem to accord very well with the evident pattern torsion in the *Ochotonidæ*. If this construction, or one similar to it, can be shown to have been a stage in the evolution of the pattern of  $P^4$  and  $M^{1-2}$  in the *Ochotonidæ* generally I need not point out to students of the *Duplicidentata* that it not only explains the chief differences in superior cheek tooth pattern in the *Ochotonidæ* and the *Leporidæ*, but also it emphasizes the early separation of the two *Duplicidentate* families.

## MEASUREMENTS\*

	<i>Desmatolagus dicei</i> C. M. No. 814 mm.	<i>Desmatolagus gazini</i> C. M. No. 37 mm.
P <sup>3</sup> antero-posterior . . . . .	2.5	2.15
P <sup>3</sup> transverse . . . . .	5.2	3.6
P <sup>4</sup> antero-posterior . . . . .	2.9	2.2
P <sup>4</sup> transverse . . . . .	6.3	4.3
M <sup>1</sup> antero-posterior . . . . .	2.5	2.15
M <sup>1</sup> transverse . . . . .	6.5	4.3
M <sup>2</sup> antero-posterior . . . . .	2.6	1.8
M <sup>2</sup> transverse . . . . .	5.6	3.4
M <sup>2</sup> transverse . . . . .	5.6	3.4
P <sub>4</sub> antero-posterior . . . . .	3.9	
P <sup>4</sup> transverse . . . . .	3.3	
M <sub>2</sub> antero-posterior . . . . .	2.9	
M <sub>2</sub> transverse . . . . .	3.1	
M <sub>2</sub> antero-posterior . . . . .	3.3	
M <sub>2</sub> transverse . . . . .	3.5	
M <sub>2</sub> antero-posterior . . . . .	1.5	
M <sub>2</sub> transverse . . . . .	1.6	
Length of inferior molar series . . . . .	10.6	

\*All measurements taken at triturating surfaces of teeth.